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Brain lateralization involved in visual recognition of conspecifics in coral reef fish at recruitment

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In vertebrates, brain functional asymmetries are widespread and increase brain performance. Some species of fishes are known to have brain asymmetries; however, little information is available on brain lateralization in coral reef fishes and the impact this could have during the recruitment phase. In this study, soldierfish, *Myripristis pralinia*, at the larval and juvenile stage recognized conspecifics through visual cues. Larvae with the ablation of either the right or left telencephalic hemisphere lost the attraction towards conspecific cues. In contrast, juveniles with the ablation of the right (but not left) telencephalic hemisphere still displayed a preference towards conspecific visual cues. These results suggest the left telencephalic hemisphere is responsible for the lateralization process used in the visual recognition of coral reef fish juveniles. The determinism of lateralized perception of conspecifics during fish ontogeny may be a consequence of genetic factors, linked with the metamorphosis processes and/or environmental factors such as predation at recruitment.

Lateralization, the preference for one side of the body over the other, is a common phenomenon in vertebrate (for a review see Salva, Regolin, Mascalzoni, & Vallortigara, 2012) and invertebrate species (for a review see Frasnelli, Vallortigara, & Rogers, 2012). Brain lateralization is thought to increase cognitive abilities, behavioural complexity or behavioural laterality, leading to advantages in brain function (Vallortigara & Rogers, 2005). Several studies have explored the role lateralization plays in emotion or cognitive decisions. For cognition, the brain's right hemisphere is responsible for processing novel items and/or items requiring a rapid response. The brain's left hemisphere is used to categorize stimuli and/or process information requiring consideration of alternatives (Rogers, Vallortigara, & Andrew, 2013). It has been suggested that the brain's ability to process positive and negative emotions utilizes the right hemisphere for both positive and negative emotional responses. Alternatively, the valence theory proposes that the right hemisphere is dominant for negative emotions and the left hemisphere is primarily used with positive emotions (e.g. Hook-Costigan & Rogers, 1998; Quaranta, Siniscalchi, & Vallortigara, 2007; Siniscalchi, Lusito, Vallortigara, & Quaranta, 2013). Empirical evidence supports the cognition and emotion theories; however, it can be argued that additional species from a more diverse group must be studied to come to any general conclusion (e.g. Jozet-Alves et al., 2012; McManus, 2005).

Most species of fishes in coral reefs have a stage-structured life history. A relatively sedentary benthic stage (juveniles and adults) produces a highly dispersive pelagic larval stage (Leis, Siebeck, & Dixson, 2011). At the end of the larval phase, organisms are required to enter the benthic reef environment, termed recruitment (Lecchini & Galzin, 2003). During this time period, species-specific

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changes in morphology and physiology, referred to as metamorphosis, occur (Leis & McCormick, 2002). Larvae lose many of the characteristics that enhanced survival in the pelagic environment, such as transparency (McCormick, 1999). In turn, once settlement occurs newly settled recruits rapidly develop features better suited for the reef habitat, such as pigmentation (Dufour, Lecaillon, & Romans, 2000). Moreover, during the recruitment phase, fish larvae are subjected to strong selective pressures to choose a suitable reef habitat that will facilitate survival and growth. Studies have documented up to 90% larval mortality in the first 7 days on the reef (Doherty et al., 2004; Lecchini, Osenberg, Shima, St Mary, & Galzin, 2007). Recruitment of new individuals is a critical process in the maintenance and recovery of marine communities (Lecchini & Galzin, 2003). Correct habitat identification depends strongly on the ability of marine larvae to recognize and respond to sensory signals from conspecifics, habitat components and predators (Barth et al., 2015). Many coral reef fish species recognize their conspecifics using visual cues (Huijbers et al., 2012; Lecchini, Peyrusse, Lanyon, & Lecellier, 2014; O'Connor et al., 2015). Despite the importance of visual, acoustic and chemical cues during the recruitment process (Leis et al., 2011), very little information is available on the relationship between brain morphology or lateralization and the behavioural and social interactions of coral reef fishes (Barth et al., 2015). A link between brain area and life history traits has been found. Indeed, nocturnally active fish species that spend less than 30 days in the pelagic environment before settling have a larger optic tectum and telencephalon than diurnal fish species that spend less than 15 days in the ocean (Lecchini, Lecellier et al., 2014). Additionally, behavioural lateralization in coral reef fish larvae is impaired by ocean acidification (Domenici et al., 2014, 2012; Nilsson et al., 2012). Few studies have explored whether lateralization could vary across the development of an individual (Concha, Bianco, & Wilson, 2012; Rogers et al., 2013; Skiba, Diekamp, & Güntürkün, 2002). Zebrafish, *Danio rerio*, 6–21 days posthatching show a significant left-eye preference when examining their reflection in a mirror (Sovrano & Andrew, 2006). Cuttlefish, *Sepia officinalis*, 3–45 days posthatching progressively develop a left turning bias (Jozet-Alves et al., 2012). Both studies indicate the development of the lateralization process during an early life history stage. Coral reef fish offer an important group of organisms to study the development of lateralization. Selection favours individuals on reefs that chose an ideal location, and the visual recognition of conspecifics provides an indication of optimal settlement sites. The use of visual cues could be favoured by the lateralization process in cognition, with larvae recognizing familiar conspecifics compared to unfamiliar heterospecifics.

Overall, understanding the ontogeny of lateralization is essential for complete comprehension of the larval recruitment processes. This is especially important as changing climate conditions impact lateralization's function (Nilsson et al., 2012). Here, we tested coral reef fish at the larval (premetamorphosis) and juvenile (metamorphosed) stage to better understand the role that lateralization plays in the cognitive recognition of visual conspecific cues. The importance of telencephalic hemispheres in the visual recognition of conspecifics was tested using behavioural assays conducted on fish with and without one or other hemisphere of the telencephalon. This determined whether the lateralization of the brain is present at the larval and/or juvenile stages during recruitment.

METHODS

Specimen Collection

Fish larvae were collected nightly from February to June 2011 and September 2014 using crest nets set on the west coast of Moorea Island, French Polynesia (17°31′03,56″S, 146°55′21,53″W). This sampling technique collects fish larvae in the process of recruitment (Lecchini, Dufour, Stand, & Galzin, 2004; Lecchini et al., 2006; Lo-Yat et al., 2011). A rectangular mouth (1 m wide, 2 m high) net (1 mm mesh) was oriented perpendicular to the water flow, designed to retain all incoming larvae (for methods see Lecchini et al., 2004). Larvae were collected between 1700 and 0600 hours, to maximize the capture of nocturnal recruiting larvae while minimizing the amount of debris collected during daylight hours (Lecchini et al., 2006). Crest nets do not target specific species.

The soldierfish, *Myripristis pralinia*, was chosen due to the high number of individuals collected (total: 148 larvae) and the biology of the species. *Myripristis pralinia* live in shoals that include all sessile ontogenetic stages: newly settled recruits, juveniles and adults (Lecchini & Galzin, 2005). Fish larvae and juveniles use vision to recognize conspecifics during recruitment (Barth et al., 2015; Lecchini, Shima, Banaigs, & Galzin, 2005). To determine the difference in lateralization between life history stages, both larvae (size: 5.8 ± 0.2 cm) and juveniles (size: 6.2 ± 0.1 cm) were tested. Juveniles were obtained by rearing collected larvae in aquaria for 7 days, which ensured that metamorphosis was finished.

Brain Surgery

To determine the importance of brain lateralization in conspecific recognition, surgery was necessary. Surgical procedures followed modified methods from Salas, Broglio, Duran, Gomez, and Rodriguez (2008) and Durán, Ocaña, Broglio, Rodríguez, and Salas (2010). Surgery on larvae was conducted within 24 h of collection. Surgery on juveniles was conducted 7 days after larval collection. An individual was first anaesthetized in 0.07 g/litre of MS222 (m-aminobenzoic acid ethyl ester, methanosulphate salt) dissolved in sea water. Once unconscious, the fish was placed in a surgical chamber. Two PVC side plates kept the fish stable during surgery. The fish was maintained alive and unconscious using a tube inserted into the mouth continuously flushing sea water containing MS222 (0.07 g/litre). The telencephalic hemispheres were exposed through four incisions on the top of the skull using conventional dissection equipment. The removed piece of the cranium was placed on wet cotton until the end of the surgery. The left or right telencephalic hemisphere was removed using a micropipette connected to a syringe. Regular verifications were made through a binocular microscope to avoid surgical mistakes. After hemisphere removal, the piece of cranium was replaced in its original position and fixed with cyanoacrylate glue. To ensure that the surgical procedure did not affect fish behaviour, the surgery was conducted on 10 individuals of each stage and the skull was closed without ablation, termed a sham operation. After surgery, the fish was woken by circulating untreated sea water through the tube inserted into the mouth. All surgeries were conducted in less than 10 min. Overall, four experimental groups of fishes were considered: nonoperated (NS), sham-operated (Sh), right telencephalic hemisphere removed (RT) and left telencephalic hemisphere removed (LT).

Visual Recognition of Conspecifics by Fish Larvae and Juveniles

The fish were behaviourally assessed using a three-compartment test chamber (60 × 12 cm and 10 cm high (Lecchini, Peyrusse, et al., 2014; Fig. 1). The side compartments consisted of two transparent Plexiglas panels separated by 1 cm placed to create barriers at 8 cm from each end, resulting in a central compartment (length: 32 cm). The central compartment was separated into three